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THE LARVAL AND POST-LARVAL DEVELOPMENT OF THE SCORPION SPIDER CRAB, INACHUS DORSETTENSIS (PENNANT) (FAMILY: MAJIDAE), REARED IN THE LABORATORY

By R. W. INGLE

INTRODUCTION

THE Scorpion Spider Crab, *Inachus dorsettensis* (Pennant), occurs from Norway, through the north Atlantic to the Mediterranean and along the west and South African coasts as far as Natal, being confined to littoral waters to depths of 550 m (Monod, 1956: 529). It is reported from hard to muddy substrates (Christiansen, 1969: 102) although in British waters it has been taken chiefly in areas of sandymud (Marine Biological Association, 1957: 260; Hartnoll, 1963: 434). In British waters this species breeds throughout the year (Lebour, 1928: 502).

Although adults of the three British *Inachus* species are readily distinguishable from each other, the larval and post-larval stages cannot be reliably identified at present because of the lack of adequate descriptions. Recently *I. dorsettensis* was reared to ninth crab stage in the laboratory and the early developmental stages are described in detail below.

MATERIAL AND METHODS

Larvae were hatched from crabs collected on or near the Eddystone Grounds, off Plymouth, Devonshire, England, and were reared using the method described by Rice & Ingle (1975: 104).

Larvae and moults were preserved in 70% alcohol and in 5% buffered formal-saline. Dissections were made in polyvinyl-lactophenol/lignin pink medium. Drawings and measurements were made with the aid of a camera lucida. The measurements taken were: dorsal spine length $(D.S.) = \text{distance between tip of dorsal spine and rostrum, and carapace length } (C.L.) = \text{distance between base of eyestalk and posterio-lateral margin of carapace. Between 5 and 10 suitable specimens of each stage were measured. Sizes given under Dimensions are those for the smallest and the largest specimens.$

RESULTS

Most females hatched their total brood within a period of 36 hours; a few took up to 48 hours. All successfully reared larvae hatched as free-swimming zoeae. The small percentage that hatched as pre-zoeae all died within 24 hours.

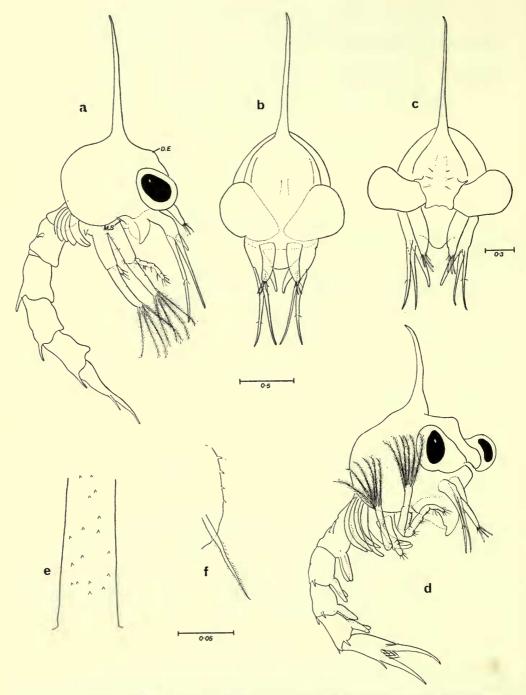


Fig. 1. Inachus dorsettensis, lateral and frontal aspects of zoeal stages: (a), (b) first zoea and (c), (d) second zoea; (e) basal part of dorsal spine of first zoea; (f) majid spine of first zoea. Scales in millimetres.

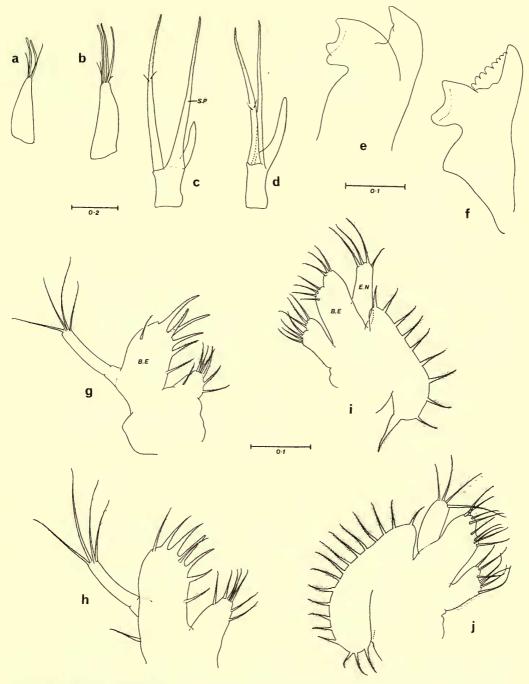


Fig. 2. Inachus dorsettensis, (a), (b) antennule; (c), (d) antenna; (e), (f) mandible; (g), (h) maxillule; (i), (j) maxilla of: (a), (c), (e), (g), (i) first zoea and (b), (d), (f), (h), (j) second zoea. Scales in millimetres.

DESCRIPTIONS

Inachus dorsettensis (Pennant)

Larval references. Inachus scorpio Claus, 1876: Taf. X, fig. 8 (1st zoea); non Inachus scorpio Cano, 1893: Taf. 35, fig. 7 (1st zoea) = I. thoracicus (Roux); Inachus dorsettensis Lebour, 1927: 795; Pl. I, figs 1, 4-6 (pre-zoea), fig. 7 (1st zoea), Pl. II, figs 1, 4-7, Pl. IV, figs 1, 3 (2nd zoea), Pl. II, fig. 10, Pl. III, figs 1, 7, 8, Pl. IV, figs 2, 4 (megalopa), Pl. III, fig. 8 (1st-3rd crab); 1928: 546, Pl. III, fig. 5 (1st zoea, col. fig.), Pl. XV, fig. 4 (1st crab), fig. 5 (2nd crab); Heegaard, 1963: 471 (1st zoea), Pl. XVII (coloured fig.), text-figs 70-76.

FIRST ZOEA

Dimensions: D.S. 1.9-2.0 mm; C.L. 0.9-1.0 mm.

Carapace (Fig. 1a, b): Dorsal spine well developed, apically curved, armed with minute spinules most numerous at base (Fig. 1e). Rostral and lateral spines absent. Dorso-median elevation (D.E.) prominent; majid spine (M.S.) plumose, arising from inner ventral carapace margin and well developed (Fig. 1f), posterio-ventral margin of carapace spinulate.

Eyes: Partly fused to carapace.

Antennule (Fig. 2a): Unsegmented with two terminal aesthetascs and 2 setae.

Antenna (Fig. 2c): Spinous process (S.P.) about $\frac{2}{3}$ length of dorsal spine, distal $\frac{1}{3}$ invested with minute spinules. Exopod as long as spinous process with 2 median spines, distal $\frac{1}{3}$ spinulate. Endopod about $\frac{1}{3}$ length of spinous process.

Mandible (Fig. 2e): Incisor and molar process developed, palp absent.

Maxillule (Fig. 2g): Endopod 2-segmented, distal segment about $4 \times$ length of proximal and with 4 distal setae; basal endite (B.E.) with 5 setosed spines and 2 setae, coxal endite with 7 plumose setae.

Maxilla (Fig. 2i): Endopod (E.N.) narrow, apex truncate with 3 long and I (outermost) short plumose setae; basal endite (B.E.) bilobed with 7-8 plumose setae; coxal endite bilobed with 7 plumose setae, inner margin invested with fine setules. Scaphognathite with 10 plumose setae, distal one very stout, posterior lobe short.

First maxilliped (Fig. 3a): Basis with 9 setae (arranged 2, 2, 2, 3), endopod 5-segmented with 3, 2, 1, 2, 4 + 1 setae respectively; exopod incipiently 2-segmented, distally with 4 terminal plumose setae.

Second maxilliped (Fig. 3b): Basis devoid of setae, endopod 3-segmented with 0, 1, 3 + 1 setae respectively, distal segment about 3× length of proximal, exopod incipiently segmented, distally with 4 plumose setae.

Third maxilliped (Fig. 3c, MX): Represented as a small unsegmented bud.

Peraeopods (Fig. 3c): Conspicuous, 1st incipiently chelate, 2nd-5th unsegmented as terminally acute finger-like projections.

Abdomen (Fig. 4a, b): 5-segmented + telson. Segments 2-5 with incipient pleopod buds; 2nd segment with pair of forwardly directed dorso-lateral processes, segments 3-5 each with a pair of long posterior dorso-lateral spines and with posterior ventro-lateral margins rounded to truncate. Posterio-dorsal margin of segments 2-5 each with a pair of small setae. Telson forks long, not diverging posteriorly, lateral spines (L.S.) long, nearly $\frac{1}{3}$ length of forks, both invested with minute spinules; each half of telson posterior margin convex, with 3 plumose setae.

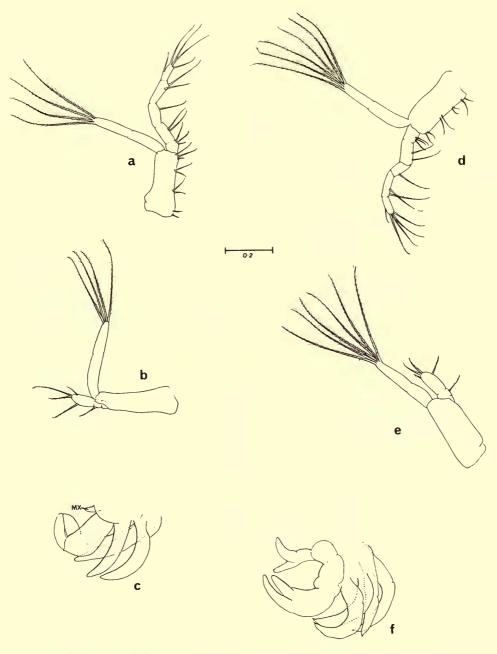


Fig. 3. Inachus dorsettensis, (a), (d) first maxilliped; (b), (e) second maxilliped; (c), (f) third maxilliped and peraeopods of: (a)-(c) first zoea and (d)-(f) second zoea. Scale in millimetres.

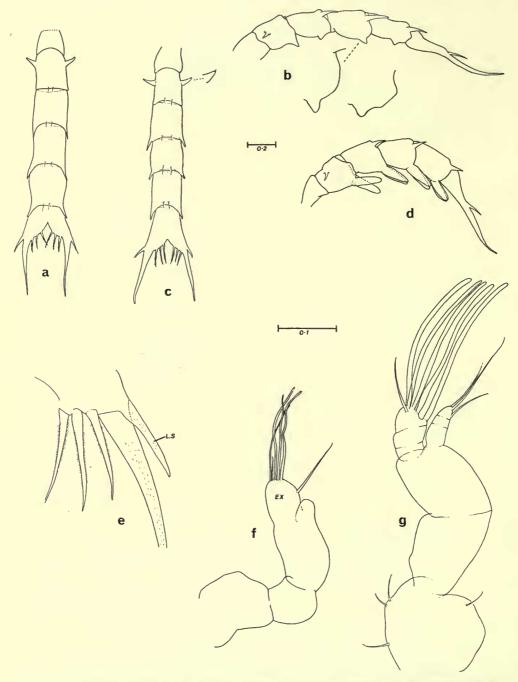


Fig. 4. *Inachus dorsettensis*, abdomen, dorsal (a), (c) and lateral (b), (d) aspects of (a), (b) first zoea and (c), (d) second zoea; (e) right half of telson of second zoea; (f) antennule of megalopa; (g) antennule of first crab. Scales in millimetres.

SECOND ZOEA

Dimensions: D.S. 1.7-1.8 mm; C.L. 1.2-1.3 mm.

Carapace (Fig. 1c, d): Dorsal spine slightly more curved and shorter than in first stage, dorso-median elevation more pronounced and now with 2 rows of 3 setae; rostrum pronounced, ocular eaves developed.

Eyes: Now stalked.

Antennule (Fig. 2b): Now with 3 terminal aesthetascs and 3 setae.

Antenna (Fig. 2d): Endopod now about ½ length of spinous process.

Mandible (Fig. 2f): Distal margin of incisor process cut into rounded teeth.

Maxillule (Fig. 2h): Outer margin of basal endite now with a plumose seta, distal margin now with 3 setae.

Maxilla (Fig. 2j): Outermost plumose seta of endopod longer than in first stage; basal endite with 9 plumose setae; scaphognathite with 17 plumose setae, distal one no longer stout.

First maxilliped (Fig. 3d): Exopod now with 6 terminal plumose setae. Second maxilliped (Fig. 3e): Exopod now with 6 terminal plumose setae.

Third maxilliped (Fig. 3f): Now a pronounced bilobed bud.

Peraeopods (Fig. 3f): 2nd-5th incipiently segmented.

Abdomen (Fig. 4c, d): Segments 2-5 with well-developed pleopod buds, dorso-lateral processes on 2nd segment longer than in first stage and with terminal spinules; posterior dorso-lateral spines shorter than in first stage; telson forks diverging posteriorly, spinules (Fig. 4e) conspicuous.

MEGALOPA

Dimensions: C.L. 1·1-1·2 mm.

Carapace (Fig. 10a): Longer than broad, narrowing anteriorly. Front with a pair of widely spaced anteriorly directed acute frontal horns and medially with an obtuse protuberance; protogastric region with 3 transverse low tubercules, outermost 2 spined; cardiac with 3 spines transversely placed, intestinal with a low posteriorly placed tubercule.

Eyes: Large and long, cornea well developed.

Antennule (Fig. 4f): Peduncle 3-segmented, exopod (EX) not demarcated from

peduncle, with 4 aesthetascs and 2 setae, endopod vestigial.

Antenna (Fig. 5d): 6-segmented, flagellum not demarcated from peduncle. First segment with ventrally directed spine and outwardly directed obtuse process, 3rd segment with I seta, 5th segment longest with 4 terminal setae, 6th with 2 long and I short terminal setae.

Mandible (Fig. 5a): Incisor process well developed, molar reduced, now with 3-segmented mandibular palp, distal segment with 1-2 setae.

Maxillule (Fig. 5b): Endopod now reduced, unsegmented; basal endite with 6

spines and 5-7 setae, spines thinner than in zoeal stages.

Maxilla (Fig. 5c): Endopod reduced to terminally acute process; basal endite slightly bilobed with 9-10 plumose setae; coxal endite slightly bilobed with 5 plumose setae. Scaphognathite with 22 plumose setae shorter than in zoeal stages. First maxilliped (Fig. 6a): Coxal endite (C.E.) bilobed, invested with 1 and 4 setae

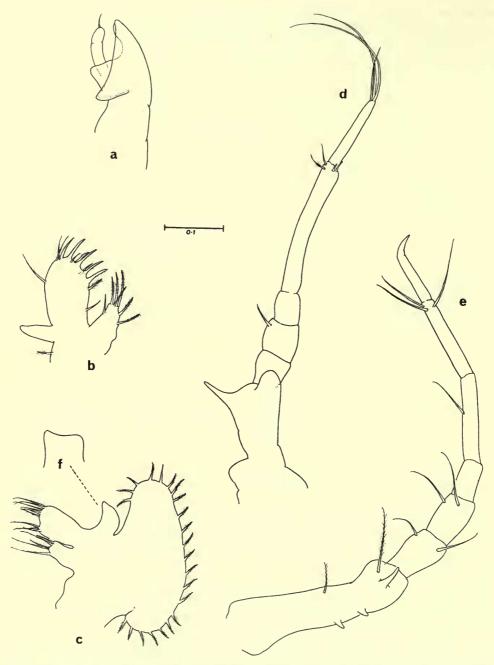


Fig. 5. Inachus dorsettensis, (a) mandible, (b) maxillule, (c) maxilla and (d) antenna of megalopa; (e) antenna and (f) endopod of maxilla of first crab. Scale in millimetres.

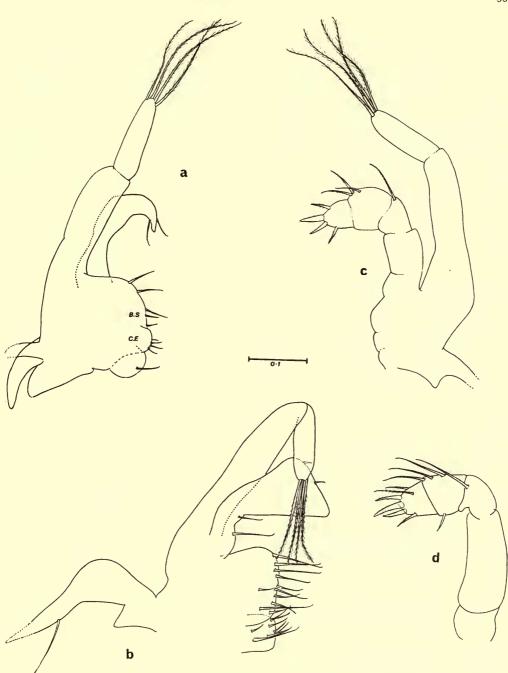


Fig. 6. *Inachus dorsettensis*, first maxilliped of (a) megalopa and (b) first crab; second maxilliped (c) of megalopa and (d) endopod of second maxilliped of first crab. Scale in millimetres.

respectively; inner margin of basis (B.S.) with 5 setae. Exopod long, stout, 2-segmented, distally with 4 long terminal plumose setae; endopod curved with 1-2 subapical setae, epipod short, bilobed.

Second maxilliped (Fig. 6c): Basal and coxal segments not separated, endopod 5-segmented, 1st segment not completely demarcated from 2nd, 3rd with 1, 4th with 3 dorso-external setae, 5th with 4 setosed spines. Exopod long, stout, 2-segmented, distal segment with 4 plumose setae, epipod short, bilobed.

Third maxilliped (Fig. 7a): Basis slightly demarcated from coxa, inner margin of coxal segment with I spine and I seta, ischium with 3-5 acute spines or processes and 6 setae with additional 2 on outer surface; merus with a small blunt anterio-internal spine on inner surface, merus to dactylus setosed as shown in figure.

Peraeopods, cheliped (Fig. 7c): Inner margin of ischium/basis with 3 stout curved spines, merus with 3 stout spines, carpus inner margin with 1 small spine, propodus distal half, inner margin sharp, slightly cristate, setal investment as shown in figure. Peraeopods 2–5 (Fig. 8b) dactylus distally spinulate, much longer than propodus + carpus, basis of peraeopods 2–3 with stout curved spine, merus of peraeopods 2–4 and sometimes ischium with long spines decreasing in size distally; setal and spinule investment as shown in Fig. 8b.

Abdomen (Fig. 8a, 10a): Sub-cylindrical 5-segmented + telson. Posterio-dorsal margins of segments 2-5 with pair of acute spines (P.D.) decreasing in size on successive segments; segment 3 with 1 pair and 4 and 5 with 2 pairs of additional minute spinules; dorsal surface of segments 2 and 3 with a median spine. A pair of well-developed pleopods on segments 2-5, exopods (Fig. 9c) long, each with 8 terminal plumose setae; endopod short with 2 coupling hooks on each pleopod.

FIRST CRAB

Dimensions: C.L. 1·4-1·5 mm.

Carapace: Longer than broad, narrowing anteriorly, invested with numerous setae of varying lengths (Fig. 10b). Anteriorly directed frontal horns broader than in megalopa, apices setosed. Hepatic and outer epibranchial regions swollen, each with a spine; meso-metagastric and cardiac regions swollen, latter with a pair of small tubercules.

Eyes: Large and broad, cornea well developed.

Antennule (Fig. 4g): Exopod now with 3 incipient segments, terminal with 5 aesthetascs and one seta; endopod with 3 incipient segments, terminal with 3 setae.

Antenna (Fig. 5e): Now 7-segmented, flagellum not demarcated from peduncle; 1st segment longest, inner margin with ventrally directed spine shorter than in megalopa and 2 additional smaller spines on inner margin, outer margin with 2 plumose setae; 2nd and 3rd segments each with 2 setae, 5th with 1, 6th with 3, 7th with apex indistinctly segmented.

Mandibles, maxillule and maxilla: As in megalopa.

First maxilliped (Fig. 6b): Coxal segment with 8 setae, no longer bilobed, demarcated from basis which has II-I2 setae, endoped distally expanded into broad lobe with 2-3 marginal setae, epipod longer than in megalopa with I-2 setae.

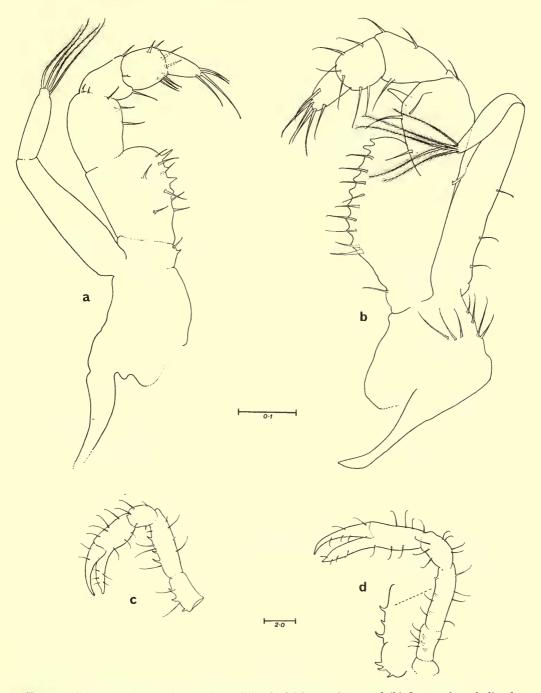


Fig. 7. Inachus dorsettensis, third maxilliped of (a) megalopa and (b) first crab; cheliped of (c) megalopa and (d) first crab. Scales in millimetres.

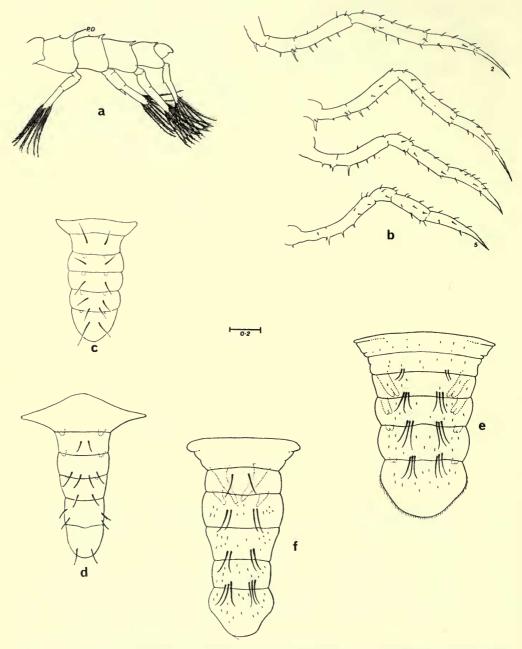


Fig. 8. Inachus dorsettensis, (a) abdomen (b) peraeopods 2-5 of megalopa; abdomen (c) of second crab, (d) of third crab 3, (e) of fourth crab 2 and (f) of fourth crab 3. Scale in millimetres.

Second maxilliped: 2nd segment of endopod longer than in megalopa (Fig. 6d), 4th segment now with 4 setae, 5th with 2 setae.

Third maxilliped (Fig. 7b): Outer margin of basis with 7-10 setae, inner margin of ischium with 9-12 acute or subacute spines and 9-12 setae; anterio-internal spine on merus now prominent, merus-dactylus setosed as shown in figure.

Peraeopods: Propodus of cheliped (Fig. 7d) less inflated than in previous stage, margins sharp. Peraeopods 2–5 similar, 2nd (Fig. 9d) longest, dactylus of 2nd-4th shorter than propodus, dactylus of 5th (Fig. 9e) same length as propodus and with inner margin bearing 1–2 broad spines, peraeopod setae long.

Abdomen (Fig. 9a, b): Sub-cylindrical, posterio-dorsal margins of segments 2-5 now with minute spinules and a pair of long setae; a minute median spine on dorsal surface of telson; pleopods reduced.

SECOND CRAB

Dimensions: C.L. 1.8-2.0 mm.

Description: Unchanged except for abdomen (Fig. 8c) which is now strongly dorso-ventrally flattened and broad. Pleopods on segments 2-5 now reduced to minute buds.

THIRD CRAB

Dimensions: C.L. 2·3-2·5 mm.

Carapace: With a pair of well-developed hepatic spines (Fig. 10c); setae investing carapace and limbs now strongly hooked at apices.

Abdomen: Male: Narrow (Fig. 8d), well-developed pleopod buds now present near posterior margins of segments 1 and 2, those on segment 3 minute; no pleopods on segments 4-5.

Female: slightly broader than that of male's; biramous pleopods present on segments 2-5, but those on segments 4 and 5 very small.

FOURTH CRAB

Dimensions: C.L. 2·8-2·9 mm.

Carapace and limbs: As in previous stage.

Abdomen: Ventral surface with more setae and margin of 6th segment setosed. Pleopods: Male – 1st and 2nd pairs (Fig. 8f) much longer than in previous stage. Female – 2nd and 3rd pairs longer than in previous stage, 4th and 5th pairs still vestigial (Fig. 8e).

FIFTH CRAB

Dimensions: C.L. 3·1-3·2 mm.

Carapace (Fig. 10d): Now with 4 transverse protogastric tubercules and 1 mesogastric; a pair of mesobranchial and 1 gastric tubercule as in the adult form.

Pleopods: Male - 1st and 2nd now well developed.

Female – Pleopods of the 4th and 5th abdominal segments now much longer and strongly biramous.

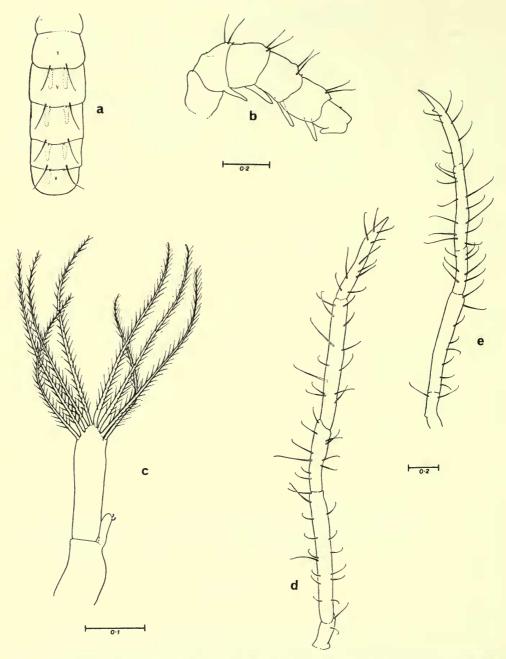


Fig. 9. Inachus dorsettensis, abdomen of first crab, (a) dorsal and (b) lateral aspects respectively; (c) 1st pleopod of megalopa; (d) 1st peraeopod of first crab; (e) 5th peraeopod of first crab. Scales in millimetres.

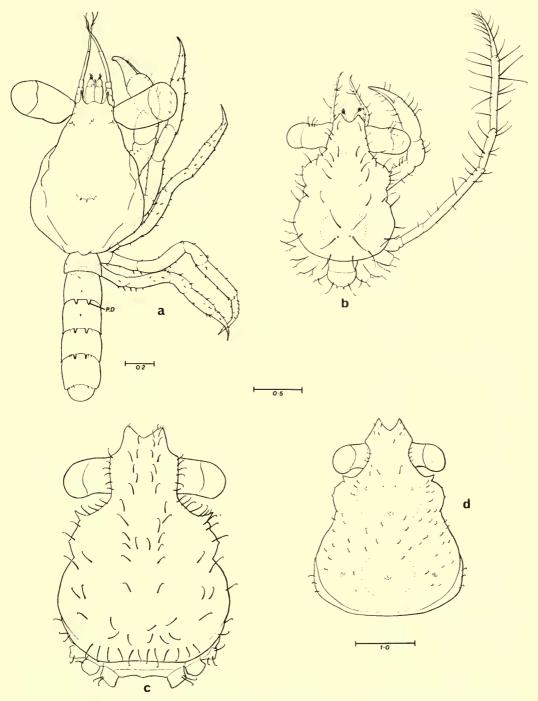


Fig. 10. Inachus dorsettensis, (a) megalopa; (b) first crab; (c) third crab; (d) fifth crab. Scales in millimetres.

REMARKS

In Tables 1 and 2 the present material of I. dorsettensis is compared with previous accounts of the larval and juvenile stages of this species. Some differences are apparent in setal armature of certain appendages of the first zoeal stages, particularly with reference to the maxillules, maxillae and maxillipeds of Heegaard's Mediterranean material.

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	Claus, 1876	Lebour, 1927; 1928	Heegaard, 1963	Ingle, 1977
Dorsal spine:	slightly longer than carapace length, curved	as long as carapace, curved	much longer than carapace, curved	slightly longer than carapace, apically curved
Majid spine: Dorso-median elevation of	not shown	not shown	well developed	well developed
carapace: Antennule:	slight 2 aesthetascs	pronounced 2 aesthetascs + 1 seta	very pronounced 2 aesthetascs + 2 setae	very pronounced 2 aesthetascs + 2 setae
Antenna, spinous process:	shorter than dorsal spine	shorter than dorsal spine	much shorter than dorsal spine	shorter than dorsal spine
Antenna, endopod, spinous process length:	about ½	about 1	between ½ and ½	about ½
Maxillule, basal endite:	not shown	not shown	with 4 setosed spines and 2 setae	with 5 setosed spines and 2 setae
Maxilla, basal endite: Maxilla, scaph-	not shown	not shown	with 8 setae	with 7-8 setae
ognathite:	not shown	not shown	with 7 setae, posterior lobe long	with 10 setae, posterior lobe short
First maxilliped, basis:	without setae (?)	without setae (?)	with 3 setae	with 2, 2, 2, 3 setae
First maxilliped, endopod: Second maxilliped,	o, I, 2, I, 3+I	(?) 0, 2, 0, 2, 3+1	2, 2, I, 2, 3+I	3, 2, 1, 2, 4,+1
endopod: Second maxilliped,	(?)	(?)	2-segmented	3-segmented
endopod setae : Abdomen, dorso-	(?) 0, 2, 2	(?) o, o, 3	0, 0, 2+1	0, 1, 3+1
lateral processes:	acute	acute	truncate	acute

These differences could be genotypic, resulting from widely separated geographical populations, or phenotypic, since Heegaard's material was reared during spring and summer when Mediterranean water temperatures are much higher than those of British waters. Differences in setal armature are more apparent when Lebour's

TABLE 2

Lebour 1927; 1928 Ingle, 1977

2nd zoea

Antennule: 4 aesthetascs + 1 long seta 3 aesthetascs + 2 long and 1

short seta

Maxillule, basal endite: plumose seta on outer margin a well-developed plumose seta

not shown on outer margin

Maxilla, basal endite: with 8 setae with 9 setae

Maxilla, scaphognathite: with 20 setae with 17 setae

Megalopa

Carapace: (?) cardiac region with a cardiac region with 3 spines

tubercule

Antennule, exopod: with 5 aesthetascs with 4 aesthetascs and 2 setae Antennule, endopod: bud well developed bud vestigial

Antenna, 1st segment: spine short, obtuse spine long, acute 3rd segment: without a seta with a seta 5th segment: with 1 seta with 4 setae

5th segment: with 1 seta with 4 setae terminal segment: with 2 setae with 3 setae n dorsal spines:

Abdomen, dorsal spines: long short

1st segment:with lateral setaewithout lateral setae3rd segment:without median spinulewith median spinule

1st crab

Carapace: almost as broad as long much broader than long

account of the second zoeal stage is compared with the corresponding stage of the present material and there are even greater dissimilarities between corresponding megalopal and first crab stages (see Table 2). Such discrepancies are not easily explained, particularly as both Lebour's larvae and the present material were reared during the same months and hatched from females collected in the same area. However, variation in laboratory reared material has received little attention (see Ingle & Rice, 1971: 284; Gonor & Gonor, 1973: 245).

The first zoeal stage figured by Cano (1893) as *I. scorpio* was referred to *I. dorsettensis* by Lebour (1927) and Heegaard (1963). But this figure clearly shows a globular carapace that is without a dorso-median elevation which are two important features of the first zoea of *I. thoracicus* and Cano's larva, therefore, clearly belongs to this latter species.

At present the larval and early crab stages of I. dorsettensis cannot be distinguished from those of I. phalangium (= I. dorynchus) or from I. leptochirus. Although Lebour (1928:548) states that the first zoea of I. leptochirus has longer lateral telsonic spines than either of the other two species and is more brightly coloured and that I. phalangium has a longer dorsal spine than I. dorsettensis, she was unable to detect differences between the megalopal stages of these three species except for the 'rostral horns' that are apparently closer together in I. phalangium and I. leptochirus than in I. dorsettensis.

An interesting result of this study of *I. dorsettensis* is that the first pair of pleopod buds of the male appear at the third crab stage and not at the second as described

by Shen (1935) for the portunid *Carcinus maenas*. It remains to be seen whether this will be the case when post-larval material of other Majids and Portunids become available for comparison.

ACKNOWLEDGEMENTS

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